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Forage productivity, species evenness and weed invasion in pasture communities

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Abstract

A long standing ecological paradigm suggests that diverse plant communities should be more resistant to weed invasion compared with plant communities that have few species. Data from three separate studies were used to test the hypothesis that increased forage species diversity reduces weed invasion in pasture communities. The first study measured weed invasion in experimentally constructed pasture communities containing 1–15 species. A second experiment conducted in the greenhouse involved sowing a common perennial weed species, curly dock (*Rumex crispus*), into forage mixtures with 5 or 10 different forage species and three monocultures. The third study investigated the relationship between weed abundance and forage diversity in 37 pastures surveyed across the northeastern United States. Consistent negative relationships between forage species diversity and weed abundance were found. The causal mechanisms explaining the negative relationships between forage diversity and weed invasion were difficult to delineate since diversity was often correlated with highly productive pasture communities. The results suggest that maintaining both productive pasture communities ($>150\,\mathrm{g\,m^{-2}}$ of aboveground biomass) and an evenly distributed array of forage species should be combined to effectively reduce weed invasion. Managing pastures for increased forage species diversity could be a useful cultural control method for weeds. Increasing the diversity of forage plants also has other ecosystem benefits to pasture communities (e.g., greater primary production, stability) beyond that of weed suppression.
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1. Introduction

A long standing ecological paradigm holds that diverse plant communities should be more resistant to invasion by weeds compared with communities having few species (Elton, 1958; Levine and D'Antonio, 1999). Two interpretations are generally used to explain this result (Wardle, 2001). The first explanation involves the idea that different species in a diverse community will use local resources more effectively and create a strong competitive environment that is difficult for weedy plants to invade (Knops et al., 1999; Naeem et al., 2000). This situation can be termed 'resource use complementarity' because the resident plant species complement each other in resource use by having different rooting depths, leaf architecture, growth rates and other characteristics. A second explanation is based on the "sampling effect" concept (Aarssen, 1997; Huston, 1997). The sampling effect is caused by the increased probability that a

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more diverse community will have at least one large, productive species that will use up the available resources in the local environment effectively (Wardle, 2001). The presence of such a productive species reduces the chance that a weedy species will successfully invade a resident plant community. Recent research suggests that both processes may operate in diverse plant communities to reduce weed abundance (Crawley et al., 1999; Dukes, 2001; Knops et al., 1999; Levine and D'Antonio, 1999; Lyons and Schwartz, 2001; Naeem et al., 2000). Some studies, however, have found that plant communities with high diversity may be more susceptible to weed invasion (Palmer and Maurer, 1997; Robinson et al., 1995; Stohlgren et al., 1999). This may occur because that same characteristics that favor high resident plant diversity (e.g., rich soil nutrients, high microhabitat heterogeneity, less environmental stress), will also favor invasive weeds.

Data from three separate studies were used to test the hypothesis that increased forage species diversity would reduce weed abundance in pasture communities: (1) In 1998, a field experiment was started to study relationships between forage diversity and yield in pasture communities dominated by cool season species. Periodic weeding of plots during the first season of the experiment revealed a negative trend between forage diversity and weed density. Following the initial field season, weed density was monitored over the next two growing seasons to determine whether this trend continued; (2) A greenhouse experiment measured germination and growth of a common weed species (*Rumex crispus* L.) into pots containing different levels of forage diversity; (3) Plant species data were analyzed from a regional survey of pastures conducted across the northeastern United States (Tracy and Sanderson, 2000).

2. Methods

2.1. Field experiment

This experiment was conducted at the Russell E. Larson Agricultural Research Center at Rock Springs, Pennsylvania, USA (40°43.24′N, 77°55.90′W). Climate at the site is mid-western, continental with annual temperature of 9.4 °C and 880 mm annual precipitation (Pennsylvania State University Weather Station, State College, PA). Soils at the site are mostly Alfisols, classified as Typic Hapludalfs in the Hagerstown series (Braker, 1981). Standard soil analyses ($n = 5$, 10 cm soil depth) by the Pennsylvania State University Agricultural Analytical Laboratory indicated a mean pH of 6.3, extractable P of 78 kg/ha and K, Mg, and Ca levels averaging 0.60, 1.44, 7.28 meq/100 g soil, respectively. Soil organic matter averaged 3.46% and soils were classified as silty clay. Existing vegetation on the plot was treated with herbicide, plowed under and then the site was disced, harrowed and packed.

Eight forage mixtures including 1–15 different forage species were created from a pool of 15 cool season (C3), forages (Table 1). The eight mixtures were made by randomly choosing species from the 15 species pool. Seed mixes were manually broadcast into 2.25 m^2 plots in May 1998. Each plot received 120 g of seed divided equally among the respective species. Plots were separated by 1.5 m alleys and arranged in a randomized complete block design having 12 blocks each with eight species mixes for a total of 96 plots. Plots were not irrigated nor fertilized during 1998. In 1999 and 2000, all plots were fertilized once in April with ammonium nitrate at an equivalent of 4.4 g N m^{-2}.

Initially, forages were allowed to establish for 2 months after planting and then mowed to a stubble height of 8 cm. Plots were mowed to the same height thereafter every 4 weeks until October. Plant clippings were removed from all plots after mowing. Forage standing crop was harvested monthly in one 10 cm × 100 cm area located near the center of each plot clipped to a 3 cm stubble height. Plant clippings were dried for 48 h at 55 °C and weighed.

Plots were weeded periodically during the first year of establishment (1998). All weeds collected from each plot in September were bagged, dried 48 h at 55 °C and weighed. During the 1999 and 2000 growing seasons, all plots were weeded each week through June and then allowed to accumulate until late September. Weed density was determined each year on 27 September by counting the number of weeds within a 1 m^2 quadrat centered in each plot. Weeds were classified as being any plant that had not been sown.

Table 1

Individual plant species and species combinations in the field experiment

Perennial grasses	Legumes	Perennial forbs	Annual forbs
(A) Orchard grass: *Dactylis glomerata* (L.)	(H) Bird's foot trefoil: *Lotus corniculatus* (L.)	(L) Chicory: *Cichorium intybus* (L.)	(N) Turnip: *Brassica rapa* (L.)
(B) Tall fescue: *Festuca arundinacea* (L.)	(I) Alfalfa: *Medicago sativa* (L.)	(M) Plantain: *Plantago lanceolata* (L.)	(O) Rape: *Brassica napus* (L.)
(C) Reed canary grass: *Phalaris arundinacea* (L.)	(J) White clover: *Trifolium repens* (L.)		
(D) Timothy: *Phleum pratense* (L.)	(K) Red clover: *Trifolium pratense* (L.)		
(E) Smooth brome: *Bromus inermis* (Leysser)			
(F) Bluegrass: *Poa pratensis* (L.)			
(G) Perennial ryegrass: *Lolium perenne* (L.)			

Species mixes

1: A
2: C, G
3: B, H, J
4: B, D, F, K
6: B, E, F, G, K, O
8: D, F, G, H, I, J, L, N
10: B, E, F, G, H, I, K, L, M, N
15: A–O

Relationships between weed density and diversity were analyzed using simple linear regression. Differences in weed density among the different forage species mixtures were analyzed using one-way ANOVA.

2.2. Greenhouse experiment

A subset of the forage species planted in the field experiment were used to test for the relationship between forage diversity and weed abundance. Six forage species combinations were used and each of these was sown with curly dock, *R. crispus*, a common perennial weed in pastures of northeastern USA (Tracy and Sanderson, 2000). The three mixtures consisted of a five species mix and two, 10 species mixtures based on the same species composition as the field experiment (Table 3). In addition to the three mixtures, three species (white clover, orchard grass, and turnip) were also grown in monoculture.

The experiment began on 25 October 1999. Species mixtures were grown in 30 litre pots (18 cm diameter) filled with potting soil. Each pot received 100 seed

equally divided among the respective forage species and 100 *R. crispus* seed. A control pot received 100 *R. crispus* seed and no forage species. All treatments were replicated six times. Pots were fertilized initially with a liquid solution of 15–30–15 (N–P–K) plant fertilizer, watered regularly and arranged in a completely random design. Plants were grown under natural lighting at $18 \pm 5\,^{\circ}\mathrm{C}$.

The percentage germination of *R. crispus* seed was measured by counting seedlings on day 25 of the experiment. No significant *R. crispus* mortality was noted before day 25. The aboveground biomass in each pot was harvested at day 65. Plants were sorted to species, dried for 48 h at $55\,^{\circ}\mathrm{C}$ and weighed. *R. crispus* standing crop and percent germination were compared among the different treatments using one-way ANOVA. Significant main effects ($P < 0.05$) were compared using Fisher's LSD test ($\alpha = 0.05$).

2.3. Pasture survey

Tracy and Sanderson (2000) surveyed 37 pastures across northeastern USA during the summer of 1998.

A modified Whittaker plot method was used to sample plant richness in each pasture (Stohlgren et al., 1995). This method measures how plant richness changes over four spatial scales (1, 10, 100 and 1000 m^2). In each pasture, one 20 m × 50 m plot was established in a random location. Nested within this 1000 m^2 plot were ten 1 m^2 plots, two 10 m^2 plots and one 100 m^2 plot. Percent cover of each species and bare ground were recorded in each 1 m^2 plot. The larger plots were then successively searched for species not found in the smaller plots. Percent importance values (%IV) were calculated from the relative frequency and cover values for each species measured in the 1 m^2 plots using the equation: %IV = relative frequency + relative cover/2. %IV gave an index of the relative importance of each species in the pasture by measuring its frequency and cover.

All plants were separated into forage species used for pasture seeding in the northeastern USA with the remaining species classified as weeds. Forage diversity was assessed using the Shannon–Weiner diversity index $H' = -\sum (p_i)(\log_2 p_i)$ (Magurran, 1988), p being the proportional relative abundance of forage species belonging to the ith species. This diversity index (H') took into account both the number of species (species richness) and how evenly they were distributed in the pasture. An index of forage species evenness (J) was calculated by dividing the Shannon–Weiner index (H') by (H'_{max}), the natural log(In) of forage species richness.

3. Results

3.1. Field experiment

The most common weeds included dandelion (*Taraxacum officinale* Webber ex Wiggins.), wood sorrel (*Oxalis stricta* L.), buckwheat (*Fagopyrum esculentum* Moench), daisy fleabane (*Erigeron annus* L. Pers.), curly dock (*R. crispus*), foxtail (*Setaria* spp.), and crabgrass (*Digitaria* spp.). In the year of establishment, aboveground weed biomass differed among the pasture mixtures (ANOVA, $F_{18,77} = 2.21$, $P = 0.009$) and was generally lower in pasture communities containing six or more species. Weed biomass was not related to forage biomass in 1998 (linear regression, $F_{1,95} = 3.19$, $P = 0.08$). In 1999 and 2000,

weed density and forage yield were negatively and linearly related ($r^2 > 0.96$, $P < 0.001$, d.f. = 1, 6). Forage species richness was negatively related to weed density in 2000 ($r^2 = 0.49$, $P = 0.05$) but not in 1999. Forage species diversity represented by Shannon–Weiner index (H') was negatively related
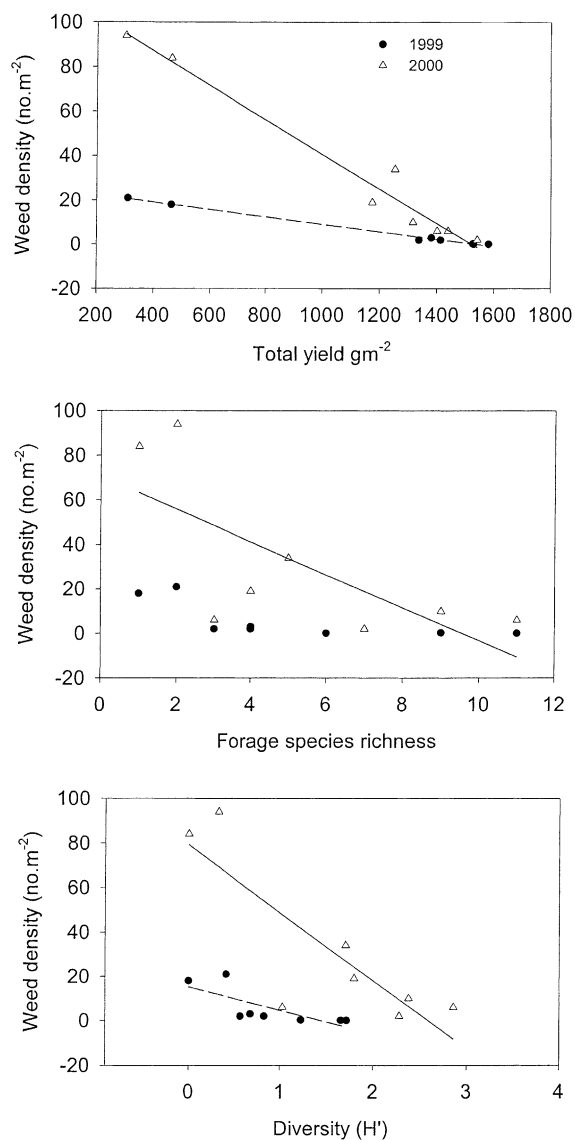

Fig. 1. Mean weed density in 1999 and 2000 in the field experiment as related to total cumulative yield over the growing season, forage species richness, and forage species diversity Shannon–Weiner (H') index ($n = 12$).

Table 2

Standing crop (g m^{-2}) at the end of greenhouse experiment (day 65)[a]

Mixture	Forage standing crop (g m^{-2})	*R. crispus* standing crop (g m^{-2})	*R. crispus* germination rate (%)
Orchard grass	105 (3.5) a	80 (9.1) a	38 (2.8) a
White clover	33 (6.2) b	89 (11) a	31 (1.8) b
Turnip	688 (27) c	0 b	19 (1.3) c
5 spp. mix	68 (9.7) ab	75 (8.1) a	28 (3.0) bc
10 spp. mix (no turnip)	177 (17) d	18 (2.0) b	22 (1.4) c
10 spp. mix (w/turnip)	487 (9.3) e	0.78 (0.53) b	20 (2.1) c
Control (*R. crispus*)	–	191 (6.4) c	60 (2.3) d

[a] Values are means ($n = 6$) and (S.E.). Means with the same letter are not significantly different based on Fisher's LSD test ($\alpha = 0.05$).

to weed density in both years ($r^2 = 0.56$ and 0.72, $P < 0.05$) (Fig. 1).

3.2. Greenhouse experiment

Standing crop among the forage treatments differed significantly (one-way ANOVA, $F_{5,30} = 346$, $P < 0.001$). Of the three monocultures, turnip standing crop greatly exceeded orchard grass and white clover (Table 2). The multiple species mixtures showed a similar trend. Standing crop of the 10 species mixture with turnip exceeded both the 5 and 10 species mixtures without turnip. The presence of forage plants repressed *R. crispus* germination and final standing crop in all cases. Percent germination and *R. crispus* biomass also differed significantly among treatments (one-way ANOVA, $P < 0.001$). *R. crispus* germination was suppressed most in the three multiple species mixtures and the turnip monoculture, but did not differ among treatments. Final standing crop of *R. crispus* was lowest in the 10 species mixtures and the turnip monoculture.

The higher standing crop of the 10 species mixture, relative to the five species mix and monocultures, was largely the result of turnip (Table 3). The 10 species mixture without turnip resulted in an increase of all species except timothy. Two broadleaf forbs, chicory and plantain, accounted for a large proportion of the standing crop in the 10 species mixture without turnip.

3.3. Pasture survey

Mean forage cover and weed importance values were negatively related in the 37 pastures surveyed across northeastern USA ($r^2 = 0.21$, $F_{1,35} = 8.77$, $P = 0.005$). Forage species richness was unrelated to weed importance value across the 37 pastures ($P = 0.77$, d.f. $= 1, 35$) (Fig. 2). Forage diversity indexed by the Shannon–Weiner index (H') was negatively related to weed importance value ($r^2 = 0.21$, $F = 9.24$, $P = 0.004$). This negative relationship may be driven by the evenness component of the diversity index, so weed importance values were

Table 3

Standing crop of individual species in each forage mixture at end of greenhouse experiment mean dry weight ($n = 6$) and (S.E.)

| Monoculture	Standing crop (g m^{-2})	5 spp. mix	Standing crop (g m^{-2})	10 spp. mix (w/turnip)	Standing crop (g m^{-2})	10 spp. mix (no turnip)	Standing crop (g m^{-2})
Orchard grass	105 (3.5)	Bluegrass	0.72 (0.32)	Alfalfa	0	Alfalfa	2.7 (0.70)
White clover	33 (6.2)	Red clover	21 (7.0)	Trefoil	0.44 (0.20)	Trefoil	1.1 (0.38)
Turnip	688 (26)	Tall fescue	30 (2.6)	Bluegrass	0.61 (0.33)	Bluegrass	1.3 (0.5)
		Timothy	9.7 (2.4)	Chicory	11 (3.6)	Chicory	81 (17)
		White clover	6.8 (1.54)	Ryegrass	5.4 (1.2)	Ryegrass	19 (3)
				Plantain	4.8 (1.2)	Plantain	38 (4.6)
				Red clover	0.72 (0.36)	Red clover	6.3 (0.9)
				Brome	2.2 (0.46)	Brome	16 (3.5)
				Tall fescue	2.8 (0.8)	Tall fescue	11 (3.6)
				Turnip	458 (13)	Timothy	0
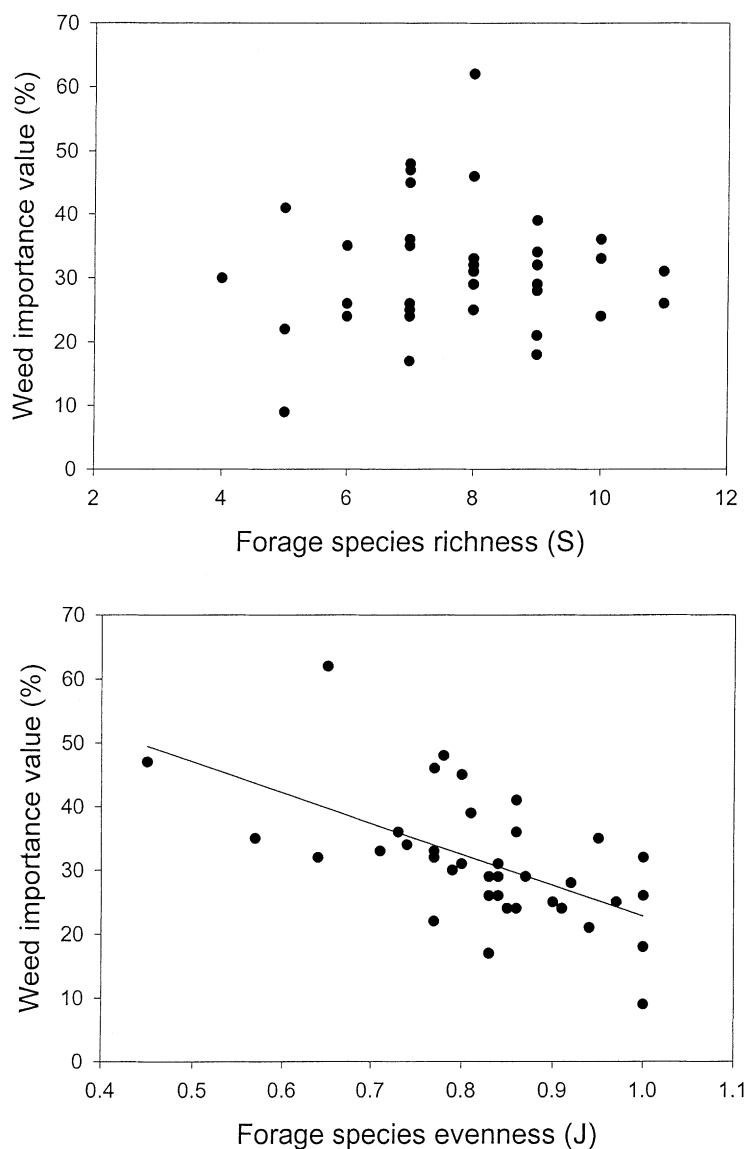
Fig. 2. Percent weed importance values from 37 pastures surveyed across northeastern United States as related to forage species richness and evenness.

regressed against forage species evenness (J) (Fig. 2). Forage species evenness was also negatively related to weed importance value and explained more of the variation compared with the Shannon–Weiner Index (H') ($r^2 = 0.35$, $F = 18.42$, $P = 0.001$). Lastly, percent forage cover and forage species evenness were positively related ($r^2 = 0.16$, $F = 6.59$, $P = 0.01$) suggesting that both variables may have a

similar, and interdependent, relationship with weed abundance.

4. Discussion and conclusion

Many experiments have reported reduced weed abundance as diversity increases in grassland

communities (Crawley et al., 1999; Knops et al., 1999; Lyons and Schwartz, 2001; Naeem et al., 2000; Wilsey and Polley, 2002). Explanations for the relationship generally fall into two categories (Wardle, 2001), i.e., (1) 'Resource use complementarity' where the different species in a community complement each other in their resource use and create a strong competitive environment that is difficult for weedy plants to invade and (2) The 'sampling effect' concept caused by the increased probability that a more diverse community will have at least one large, productive species that uses all available resources and suppresses weed invasion.

In experimental grassland communities ranging from 1 to 24 species grown at Cedar Creek Minnesota, USA, Knops et al. (1999) and Naeem et al. (2000) contended that the lower weed abundance in diverse communities was best explained by resource use complementarity. Wardle (2001), however, suggested that their findings could be explained better by the sampling effect. In the present field experiment, weed density showed strong negative and linear relationships to both forage biomass and forage diversity as indexed by the Shannon–Weiner index (H').

In the greenhouse experiment, increased forage diversity did not severely affect *R. crispus* germination. Forage biomass in the 10 species mixtures, especially those with turnip, clearly suppressed growth of *R. crispus* plants. Lower weed biomass in the 10 species mixtures with turnip, might be better explained by the sampling effect. Turnip is a good example of a 'smother crop' sometimes used to control weeds in agronomic systems (Teasdale, 1998). Although turnip may effectively control weeds, it may have some unwanted consequences on grazing animals that need a variety of forages to balance their nutritional requirements and regulate intake of toxins (Provenza, 1996). Monocultures of productive, forage plants may also be more susceptible to environmental stresses like drought, insect attack or pathogen infection compared with mixtures (Altieri, 1999). Overall, forage monocultures may produce some immediate benefits in grazing lands, but they may not be sustainable in the long run.

When turnip was removed from the 10 species mixtures, the overall aboveground biomass was high, but the biomass was more evenly spread among the different species compared with the turnip dominated mixture. Weed suppression in the 10 species mixture without turnip was likely influenced by another productive species that dominated the mixtures, chicory. *R. crispus* biomass in the five species mixture was no different than in both orchard grass and white clover monocultures. This suggests that any diversity effects may not operate in communities having less than $150\,\mathrm{g\,m^{-2}}$ in aboveground biomass. Data from the field experiment support this finding as the one and two species mixtures had significantly higher weed density compared with the other diversity mixtures in both years. Below $150\,\mathrm{g\,m^{-2}}$, resource availability (e.g., light, soil moisture) may be high enough to allow weed establishment regardless of forage species diversity.

At the pasture scale, negative relationships were found between forage diversity and weed abundance. This finding is in contrast to some studies that found positive associations between plant community diversity and weed density at large spatial scales (Palmer and Maurer, 1997; Planty-Tabacchi et al., 1996; Robinson et al., 1995; Stohlgren et al., 1998). Weed abundance was also negatively related to the Shannon–Weiner species diversity index (H') but not species richness. Forage species evenness actually explained more of the variation in weed density than the Shannon–Weiner index (21% vs. 35%). The fact that weed abundance was better explained by forage evenness and not species richness suggests that the evenness at which forage species are distributed within a pasture may be important in reducing weed abundance. Possibly, species that are evenly distributed in space may use resources more equitably and produce a competitive environment that is difficult for weeds to invade (Lyons and Schwartz, 2001; Wilsey and Polley, 2002; Wilsey and Potvin, 2000). Wilsey and Polley (2002) directly manipulated species evenness in semi-arid grassland communities while controlling for compositional effects and also found negative relationships between species evenness and weed invasion in the plots. Other factors like soil disturbance, soil fertility, and propagule supply, can also affect weed invasion at pasture scales. In native tall grass prairie communities, exotic weed invasion strongly depended on the number of weed species that surrounded the native plant communities (Smith and Knapp, 2001). Soil fertility could have influenced the relationship between weed abundance and forage diversity. More fertile, productive, pastures could be more resistant to

weed invasion if they supported a large, competitive forage biomass. To address this idea, soil phosphorus levels collected from the pasture survey (Tracy and Sanderson, 2000) were regressed against weed importance values, but there was no significant relationship ($r^2 = 0.09$, $F = 3.7$, $P = 0.06$) suggesting that soil fertility played a minor role in explaining the variation in weed abundance. Pasture age, mean precipitation, and soil texture were also unrelated to weed abundance in the survey ($P > 0.05$).

The three separate studies provided evidence to support the hypothesis that increased forage plant diversity may suppress weed invasion in pastures. The specific mechanisms for weed suppression in the pasture communities were difficult to define since forage diversity was often correlated with high productivity. The inclusion of highly productive annual forages in mixtures appeared to have a strong suppressive effect on weed invasion. Even though productive annual forages would be useful for controlling weed invasion in grazing lands, they may not be sustainable particularly in monoculture. Increasing the diversity of forage species in grazing lands could have other beneficial effects beyond weed suppression. Recent research suggests that increasing the diversity of grasslands could improve primary production, increase yield stability, reduce nutrient losses, reduce pathogen infection and possibly improve grazing animal performance (Hector et al., 1999; Hooper and Vitousek, 1998; Knops et al., 1999; McNaughton, 1977; Provenza, 1996; Tilman and Downing, 1994; Tilman et al., 1996). Overall, the present results suggest that maintaining productive pasture communities over $150\,\mathrm{g\,m^{-2}}$ of aboveground biomass and an evenly distributed array of forage species may effectively reduce weed invasion. Increasing forage species diversity could be a potentially useful cultural method for controlling weeds in pasture ecosystems.

Acknowledgements

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